EFFECT OF TEMPERATURE ON ENERGY REQUIREMENTS AND NORTHWARD DISTRIBUTION OF THE BLACK-BELLIED TREE DUCK

Brian W. Cain

A buildup in the south Texas breeding population of Black-bellied Tree Ducks was first noticed in 1955 (Henze, 1962). Further expansion of this species' breeding range may possibly be limited by competition with Wood Ducks (*Aix sponsa*) or the exotic Muscovy Duck (*Cairina moschata*) as suggested by Bolen (1971).

Temperature was suggested by Kendeigh (1944) as one of the most important environmental factors controlling a species distribution. The energy requirements of Black-bellied Tree Ducks may be a major limiting factor to their northern breeding-range extension. According to Janzen's (1967) suggestion, the tropical Black-bellied Tree Duck may not be able to tolerate a range of environmental temperatures as extreme as temperate waterfowl.

The objectives of this study are to determine the effect of temperature on the energy requirements of this species and to compare these with other waterfowl, specifically the Canada Goose (*Branta canadensis*) and the Blue-winged Teal (*Anas discors*).

METHODS

Adult tree ducks were captured near Kingsville, Texas, transported to Illinois, and placed in metabolism cages similar to those described by Owen (1970) but enlarged to 54 × 43 × 48 cm. Two weeks were allowed for the ducks to adjust to these cages. A series of constant temperatures between –20°C and 42°C were used with photoperiods similar to the winter (11 hours) and breeding (15 hours) seasons in south Texas. Humidity was not controlled in the large walk-in cabinets used as environmental chambers but was low enough at warm temperatures so as not to affect metabolism (Salt, 1952).

At 2- or 3-day intervals the ducks were fed 300 g of milo (*Sorghum vulgare*) that was oven-dried (65°C) to a constant weight. The ducks were weighed to the nearest 0.1g on a triple-beam balance. Both the unused food and the excreta were collected at 2- or 3-day intervals and oven dried at 65°C to a constant weight. Caloric values were determined with a Parr oxygen bomb calorimeter.

The relationship between photoperiod, temperature, and metabolism were determined using the method developed by Kendeigh (1949). This procedure involves subtracting the caloric value of the excreta (excretory energy) from the caloric value of the food eaten (gross energy intake). This value is the amount utilized (metabolized energy) and during a period of constant weight (change within ± 1.5 percent) is called existence metabolism. As the temperature was lowered and the birds gain weight, the existence energy measurements were made only after the birds stabilized at the new weight.

Limits of temperature tolerance were determined by lowering or raising the temperature

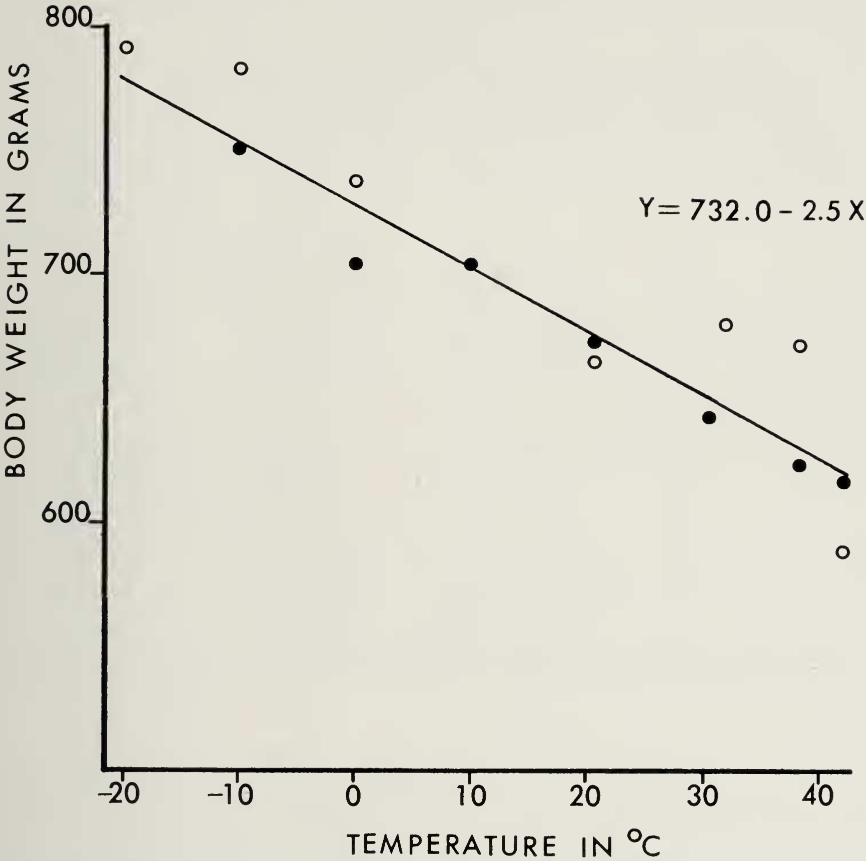

Fig. 1. The linear relationship between body weight and temperature. Solid circles represent the 11-hour photoperiod and the clear circles the 15-hour.

2°C at 3-day intervals until the tree ducks died or could not maintain constant weight. The initial temperature that the tree ducks were acclimated to before these experiments started was 35°C for the upper limit and 0°C for the lower limit.

A probability level of 0.05 was required for significance. Statistical analysis included least squares linear regression with F-values for significance and t-test between means.

RESULTS

Body Weight.—The body weight of Black-bellied Tree Ducks increased as the temperature was lowered (Fig. 1). Weights at the 11-hour photoperiod were generally lower than at 15-hours but were not significantly different. The weights of all caged tree ducks were lower than the average of 72 free-living adults (i.e. 827.8 g) measured by Bolen (1964).

TABLE 1

GROSS ENERGY INTAKE (GEI), EXCRETORY ENERGY (EE), AND THE UTILIZATION COEFFICIENTS (UC) FOR ADULT TREE DUCKS AT TWO PHOTOPERIODS. Energy expressed as kcal/bird-day and parentheses enclose ± 2 standard errors.

Temperature	N	GEI	EE	UC
11-hour				
38	10	81.9 (10.1)	12.9 (1.6)	84.0 (0.9)
30	12	*96.2 (7.7)	*17.7 (1.5)	81.5 (1.3)
20	20	*160.0 (14.5)	*25.1 (2.4)	84.1 (0.3)
10	5	*181.0 (20.8)	28.8 (3.6)	84.1 (1.0)
0	8	*226.9 (27.8)	*39.4 (6.0)	82.2 (2.7)
-10	7	*258.5 (16.7)	39.4 (1.8)	84.3 (1.1)
15-hour				
42	8	84.4 (10.5)	13.5 (1.8)	83.9 (0.7)
38	5	*114.3 (8.2)	17.0 (2.7)	85.2 (1.3)
32	8	*125.5 (15.5)	16.8 (2.8)	86.6 (1.7)
25	7	128.1 (18.4)	16.8 (3.0)	86.9 (1.5)
21	24	*163.0 (12.4)	*21.7 (1.5)	86.2 (1.1)
0	11	*259.4 (23.9)	*38.2 (4.8)	85.9 (0.6)
-10	7	*331.3 (12.0)	*48.9 (1.6)	85.2 (1.1)
-20	5	376.1 (31.6)	*54.3 (4.4)	85.4 (1.6)

* The difference between the value at this temperature and the preceding one is significant at $P = .05$.

Males and females did not differ significantly in body weight during the metabolic trials. However Canada Geese (Williams, 1965) and Blue-winged Teal (Owen, 1970) males were heavier than their respective females at all temperatures and photoperiods.

Gross Energy Intake.—Gross energy intake increased with lowering temperatures at both photoperiods (Table 1). These linear relationships are expressed by the equations, $Y = (224.9 - 3.70\ X) \pm 59.48$ and $Y = (268.9 - 4.68\ X) \pm 59.50$ for the 11- and 15-hour photoperiods respectively. The slopes and elevations of these lines are significantly different and may reflect the greater amount of activity and a longer maintenance of high body temperature at the longer photoperiod, as suggested by Kendeigh (1969) for other birds.

Excretory Energy.—Excretory energy increased in a linear relationship with decreasing temperatures (Table 1). These relationships for the 11- and 15-hour photoperiods are expressed by the equation $Y = (34.9 - 0.56\ X) \pm 6.4$ and $Y = (38.6 - 0.65\ X) \pm 9.6$ respectively. The elevations of these lines are different but the slopes are not significantly different. Excretory energy shows similar relationships to temperature in Canada Geese (Williams, 1965) and passerine birds (Kendeigh, 1969; Davis, 1955; and West, 1960).

The caloric values of the feces from Black-bellied Tree Ducks averaged 4.2 ± 0.8 kcal/g. The values were slightly higher for birds on the 11-hour photoperiod but not significantly different. There was no relationship between temperature and the caloric value per gram of feces. Canada Geese showed a decreasing caloric value per gram of excrement with decreasing temperatures (Williams, 1965). Owen (1970) reported higher caloric values at intermediate temperatures (0° to 30°C) and lower values at the high and low extremes for Blue-winged Teal.

Utilization Coefficient.—The utilization coefficient is the ratio of metabolized energy to gross energy intake. These coefficients were lower and more variable for the 11-hour than for the 15-hour photoperiod (Table 1). Significant differences occurred at 0°, 20°, and 30°C between the two photoperiods. On the 15-hour photoperiod the coefficients were higher at intermediate temperatures and lower at both high and low temperature extremes. This is reversed to the response of Canada Geese (Williams, 1965) and Blue-winged Teal (Owen, 1970).

Existence Metabolism.—Existence metabolism increased with decreasing temperature is a linear relationship for 11- and 15-hour photoperiods (Figs. 2 and 3). The regression lines are significantly different both in slope and elevation. A steeper slope for the 15-hour photoperiod indicates that summer-acclimated tree ducks are more sensitive to decreasing temperature than those winter acclimated.

The difference in elevations of the two regression lines may be due both to increased activity at the longer photoperiod and a decrease in feather insulation. Some molting of body feathers occurred while the tree ducks were acclimating to the longer photoperiod. No measurement of insulation values of the two plumages were made in this study.

Existence metabolism for Blue-winged Teal (Owen, 1970) and Canada Geese (Williams, 1965) at temperatures above 0°C did not differ between 12- and 15-hour photoperiods. Only at high temperatures (38° and 42°C) was the difference in existence metabolism between the 11- and 15-hour photoperiods significant for Black-bellied Tree Ducks.

Temperature Tolerance.—The lowest tolerated temperature by adult tree ducks is –20°C. Below –15°C the legs of male ducks froze stiff within 3 days. Females endured –20°C for 3 days before their legs froze. One male and one female died within 24 hours after their legs froze. No tree duck survived more than 4 days after its legs froze, even if removed to above 0°C. There was no apparent difference in cold tolerance between photoperiods.

Two of six adults left outdoors in a semi-wild condition on the Vivarium ponds at the University of Illinois died after 4 days of –12°C. These two birds were not allowed into the pond's open water by the other four. The

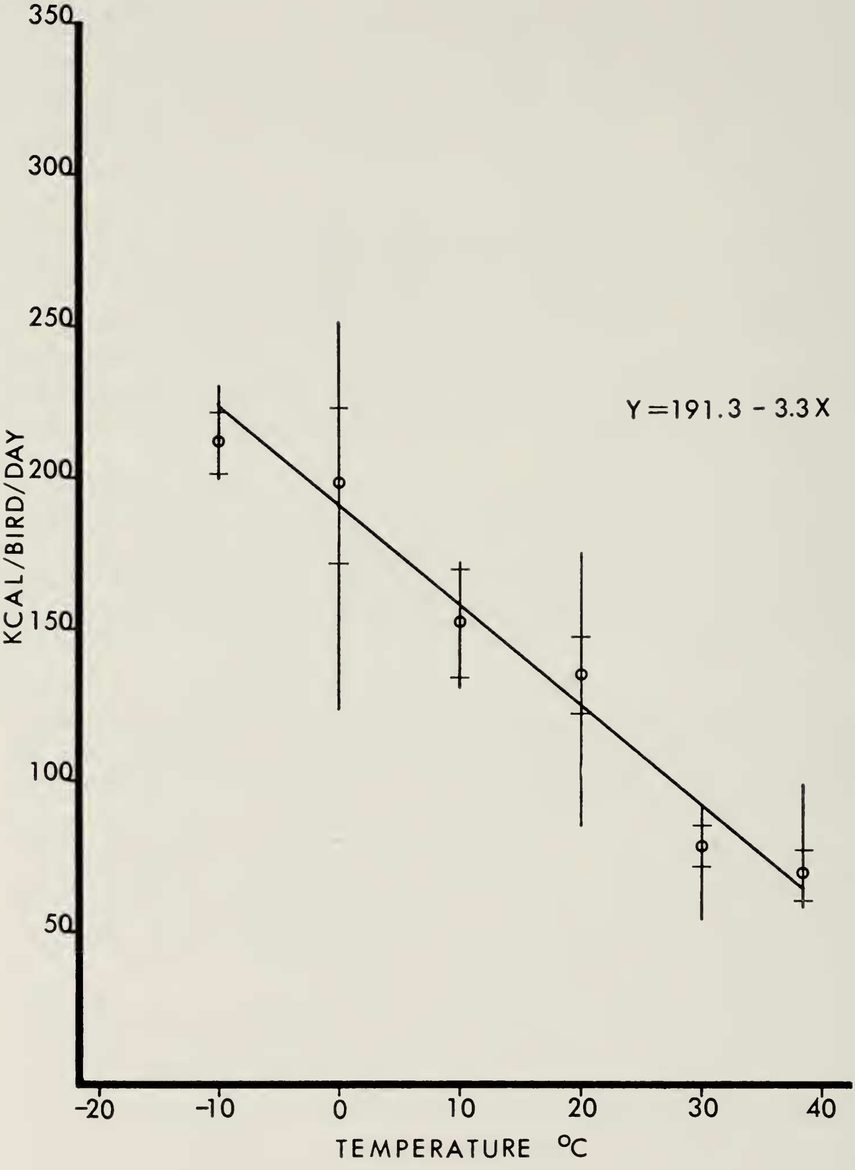

Fig. 2. Relationship between existence energy and temperature at an 11-hour photoperiod. The vertical line is the range, the circle the mean, and the two bars are ± 2 standard errors.

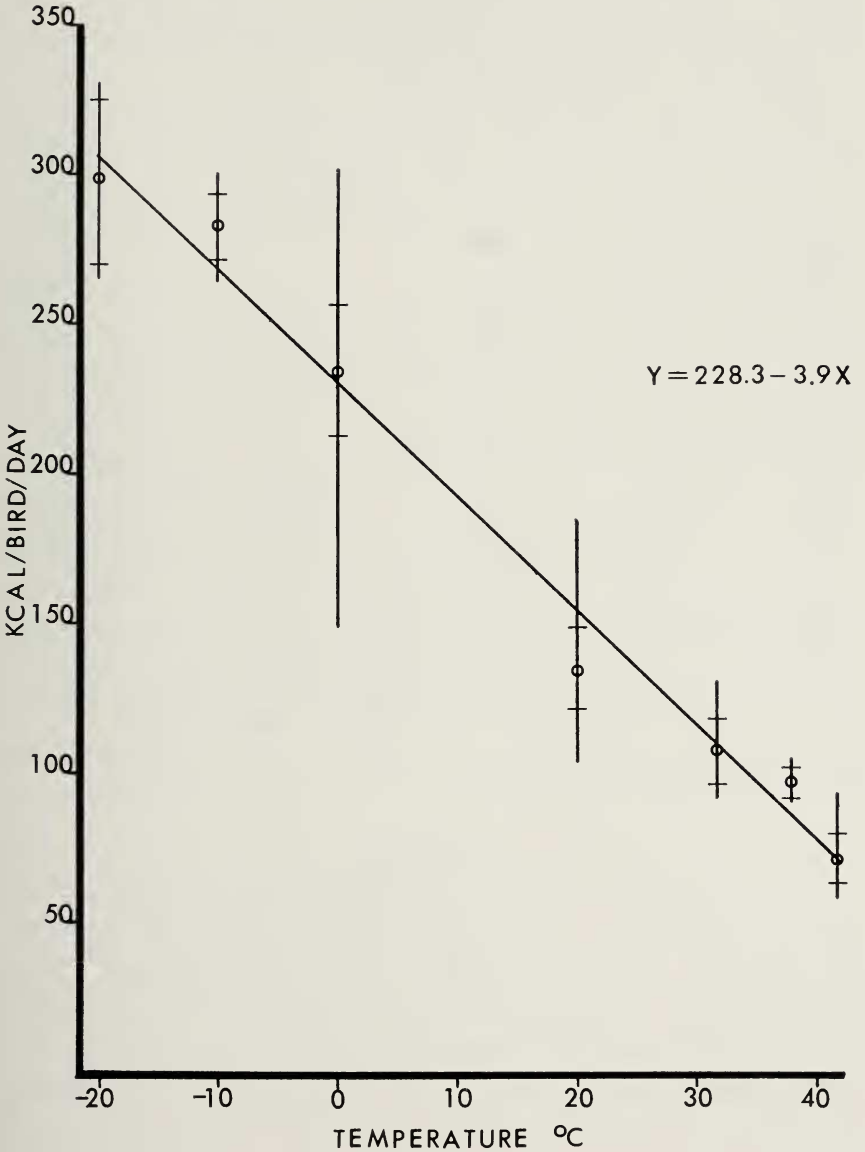

Fig. 3. Relationship between existence energy and temperature at a 15-hour photoperiod. Symbols as on Fig. 2.

open water was maintained by an inflow of water at 5°C. Canada Geese (Williams, 1965) and Blue-winged Teal (Owen, 1970) withstood –40°C without apparent physical stress. Gulls are also capable of tolerating extreme low temperatures (Scholander, et al., 1950).

Adult Black-bellied Tree Ducks at both 11- and 15-hour photoperiods lost 23 percent of their body weight within 9 days when they were exposed to 42°C. One of the four ducks at 15-hour photoperiod died, and two were obviously weakened as evidenced by their lack of activity. No panting or gular fluttering was noticed. Tree ducks at 11-hour periods were also weakened but to a lesser extent.

Canada Geese could not tolerate constant temperatures of 40–43°C (Williams, 1965). However Blue-winged Teal tolerated temperatures up to 48°C (Owen, 1970). The tropical Black-bellied Tree Duck shows evidence then of having a narrower temperature tolerance than temperate waterfowl, thus supporting Janzen's (1967) suggestion.

Maximum Potential Metabolism.—Maximum potential metabolism occurs at the lower limit of temperature tolerance (Kendeigh, 1969). Substituting –20°C, the lowest tolerated temperature, into the regression equations (Figs. 2 and 3), the maximum potential metabolism is 277 kcal/bird-day and 307 kcal/bird-day for the 11- and 15-hour photoperiods respectively. These values must be accepted conditionally as the bird's death was hastened by the freezing of its legs and not certainly due to intolerable metabolic stress. These values must be very near the maximum, however, because the efficiency of utilization had begun to drop and the birds stopped gaining weight at –20°C. The two ducks that died outdoors did not show indications of their legs being frozen the day before they died at –12°C.

DISCUSSION

Existence metabolism for free-living birds has been estimated to cost an additional 50 percent over cage existence (Kahl, 1964, and Uramoto, 1961). Blue-winged Teal, not able to fly, used 13 percent more metabolized energy in a semi-wild condition (Owen, 1970). To include the energy cost of flight I am assuming an additional minimum cost of 25 percent for free existence in Black-bellied Tree Ducks. Free-living metabolism was calculated for a 15-hour photoperiod at 3 locations in Texas (Table 2). Two of the locations are within the breeding range of this species and the other, Dallas, is 4° north of this range. The difference between the maximum potential and free-living metabolism at any temperature gives the potential productive energy at that temperature which is available for reproduction and other activities associated with survival of the individual.

The expected free-living metabolism is 173 and 157 kcal/bird-day for

TABLE 2

THE PREDICTED FREE-LIVING METABOLISM (FLM) AND POTENTIAL PRODUCTIVE ENERGY (PPE) AT THREE LOCATIONS IN TEXAS.

The energy values expressed at kcal/bird-day were calculated by extrapolation between 11- and 15-hour photoperiods.

Geographic location	Month of Year	Mean temp.[1] °C	FLM	PPE
Dallas	March	13.9	227	80
Kingsville		21.7	179	128
Harlingen		22.2	176	131
Dallas	April	18.9	192	115
Kingsville		20.6	184	123
Harlingen		22.8	173	134
Dallas	May	22.8	173	134
Kingsville		26.1	160	150
Harlingen		26.1	160	150
Dallas	June	27.2	151	156
Kingsville		28.3	146	161
Harlingen		26.7	154	153
Dallas	July	30.0	138	169
Kingsville		29.4	141	166
Harlingen		27.8	149	158

[1] From "Climatological Data-Texas Section: U.S. Dept. Commerce, Wash., D.C.

the month of May at Dallas and Kingsville, Texas, respectively. Subtracting these values from the maximum potential metabolism leaves 134 and 150 kcal/bird-day as the potential productive energy for these two locations during May (Table 2). This month was selected for calculations because the Black-bellied Tree Duck begins egg laying in May (Bolen, 1967).

Caloric values of Black-bellied Tree Duck eggs averaged 100.5 kcal (Cain, 1972). If this represents 80 percent efficiency (see Brody, 1945), the energy cost of producing one egg per day would be 125 kcal/bird-day. Subtracting this value from 134 kcal/bird-day leaves 9 kcal/bird-day surplus energy for tree ducks as far north as Dallas, Texas. This may be too narrow a margin to insure successful egg laying because a drop of only 2.5°C below the average monthly temperature, used for these calculations, would require an additional 9.7 kcal/bird-day.

It thus appears that the northward distribution of the Black-bellied Tree Duck may be limited by low temperatures decreasing the amount of energy available for successful reproduction in the spring. There is a need for research to determine if a delayed nest initiation would still permit time for egg-laying, incubation, and successful raising of broods prior to low temperatures in November at more northerly latitudes.

SUMMARY

Energy requirements of Black-bellied Tree Ducks were studied at 2 photoperiods (11- and 15-hours) and a series of temperatures between –20°C and 42°C. Body weight did not differ significantly between sexes or photoperiods but increased with decreasing temperatures at both photoperiods.

Gross energy intake, excretory energy and existence metabolism increased linearly with decreasing temperature. Existence metabolism increased more rapidly with decreasing temperature for birds on the 15-hour photoperiod.

Black-bellied Tree Ducks could not tolerate –20°C in a caged condition beyond 3 days. Their legs froze stiff and death followed within 24 hours. High temperature (42°C) resulted in a 23 per cent loss of body weight within 9 days.

Temperature may limit the northward distribution of the Black-bellied Tree Duck's breeding-range by restricting the amount of productive energy available for egg formation. Research is needed to determine the effects of other factors that contribute to this limitation.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS, CHAMPAIGN, ILLINOIS. (PRESENT ADDRESS: DEPARTMENT OF WILDLIFE AND FISHERIES SCIENCES, TEXAS A&M UNIVERSITY, COLLEGE STATION, TEXAS 77843). 25 SEPTEMBER 1972.

PUBLICATION NOTES AND NOTICES

Birds of Pennsylvania: When and Where to Find Them. (2nd Ed.) By Merrill Wood, The Pennsylvania State University, Agricultural Experiment Station, University Park, 1973: 4½ × 8½ in., paper covered, [xxi] + 103 pp., 186 drawings by Dorothy L. Bordner. $2.00.

This is an updated version of the 1967 edition (reviewed, Wilson Bull, 81:342, 1969). Brief paragraphs give frequency, abundance, seasonal occurrence, habits, status changes, and general ranges for 378 species. The reduction of 14 species since 1967 comes partly from the recent changes announced by the AOU Check-list Committee and partly by a somewhat more rigorous standard of acceptance of records.—G.A.H.